

Noctilio leporinus. By Craig S. Hood and J. Knox Jones, Jr.

Published 27 April 1984 by The American Society of Mammalogists

Noctilio Linnaeus, 1766

Noctilio Linnaeus, 1766:88. Type species *Noctilio americanus* Linnaeus.

Celaeno Leach, 1821:69. Type species *Celaeno brooksiana* Leach.
Dirias Miller, 1906:84. Type species *Noctilio albiventer* [= *albiventr*] Spix.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Superfamily Phyllostomoidea, Family Noctilionidae. The genus *Noctilio* contains only two species; they may be distinguished on the basis of characters discussed in the account that follows.

***Noctilio leporinus* (Linnaeus, 1758)**
Greater Bulldog Bat

[*Vespertilio*] *leporinus* Linnaeus, 1758:32. Type locality "America"; restricted to Suriname by Thomas (1911:131).

Noctilio leporinus Gray, in Griffith et al., 1827:67; first use of current name-combination.

Vespertilio Minor Fermin, 1765:9. Type locality Suriname.

Noctilio americanus Linnaeus, 1766:88. Type locality tropical South America.

Vespertilio labialis Kerr, 1792:93. Type locality "Vallee d'Ylo" (Valle de Ilo), Perú (but see restriction by Hershkovitz, 1949:434, and subsequent discussion by Hershkovitz, 1975:242-247).

Vespertilio mastivus Vahl, 1797:132. Type locality St. Croix, Virgin Islands.

[*Noctilio*] *rufescens* Olfers, 1818:225. Type locality Paraguay.

Noctilio unicolor Desmarest, 1818:15. Type locality South America, probably Brazil.

Noctilio dorsatus Desmarest, 1818:15. Type locality "l'Amerique meridionale."

Noctilio vittatus Schinz, 1821:870. Type locality unknown (possibly a renaming of *dorsatus*).

Celaeno brooksiana Leach, 1821:70. Type locality unknown.

Noctilio rufus Spix, 1823:57. Type locality Amazonian Brazil.

Noctilio rufipes D'Orbigny, 1835:pl.9. Type locality Río San Miguel, Guarayos, Bolivia.

CONTEXT AND CONTENT. Same as for genus *Noctilio* above. *N. leporinus* contains three recognized subspecies (Davis, 1973):

N. l. leporinus (Linnaeus, 1758:32), see above (*americanus* Linnaeus, *brooksiana* Leach, *dorsatus* Desmarest, *labialis* Kerr, *minor* Fermin, *rufus* Spix, *unicolor* Desmarest, and *vittatus* Schinz are synonyms).

N. l. mastivus (Vahl, 1797:132), see above (*mexicanus* Goldman is a synonym).

N. l. rufescens Olfers, 1818:225, see above (*rufipes* D'Orbigny is a synonym).

DIAGNOSIS. The family Noctilionidae contains only the genus *Noctilio*, in which two species, both occurring in the New World tropics, are recognized. *Noctilio leporinus* resembles *N. albiventris* (Davis, 1973, 1976; Hood and Pitocchelli, 1983) in most external and cranial features but is larger. The hindfoot of *N. leporinus* is longer than 25 mm (less than 20 mm in *N. albiventris*), tibia and hindfoot combined longer than 50 mm (less than 40 mm), forearm longer than 75 mm (less than 70 mm), wingspan about 500 mm (about 400 mm), and weight more than 50 g (less than 40 g). The cranium is larger and heavier in *N. leporinus*, although there is slight overlap between the smallest adults of that species and the largest known specimens of *N. albiventris* in most cranial mea-

surements. Length of the maxillary toothrow is rarely less than 9.0 mm in *leporinus* and rarely more than 8.0 mm in *albiventris*. The long hindlimbs, large feet, and well-developed claws in *N. leporinus* are more advanced than in *N. albiventris*.

GENERAL CHARACTERS. External characteristics include muzzle and nose without excrescences, but with strongly projecting nose pad; lips full and swollen; chin with well-developed cross ridges imparting a "bulldog-like" appearance (Fig. 1); internal cheek pouches present; ears separate, narrow, and pointed, tragus pinnately lobed with fingerlike projections; tail more than half as long as femur, extending about one-third length of interfemoral membrane, tip free of dorsal surface of membrane; hindfeet large and robust, feet and claws greatly enlarged (Fig. 2), calcar well developed and bony; humerus with trochiter smaller than trochin, articulation with scapula slight; epitrochlea and spinous process of humerus well developed and capitulum off line with humeral shaft; seventh cervical vertebra not fused with first thoracic; pelvis with ischia fused and in contact with laterally compressed, urostyle-like sacrum.

Skull lacking distinct postorbital processes; premaxillaries with nasal and palatal branches fused together and with maxillaries; palate complete and closed anteriorly; form (Fig. 3) characteristic with high, deep braincase, prominent flaring shelflike mastoids, and distinctive sagittal crest (greatly developed in males); rostrum only half as long as braincase, highly arched; nares nearly tubular, opening forward with a slight posterior emargination; palate distinctly concave when viewed laterally, but flat antero-posteriorly; maxillary toothrows nearly parallel; auditory bullae relatively small, but covering about half of cochlea.

Upper incisors crowded at midline between canines; inner pair twice as high as long, subterete and with posterior heel, their shafts curving outward distally (but strongly in contact at about middle); outer pair small and slightly behind the inner pair, their single cusps barely extending above cingulum of the inner teeth. Lower incisors equal, crowded at midline between canines; crowns longer than high and broad as long, narrow posteriorly, the upper surface concave, but not deeply bilobed. Upper canines high and short, with distinct, extremely oblique cingulum, no secondary cusps, and inner surface slightly concave with median ridge, the outer surface uniformly convex. Lower canines with slight twist in shaft near middle. Upper premolar nearly parallel-sided, crown twice as broad as long, with well-developed cusps. First and second upper molars subequal, with cusps, styles, and commissures all well developed; posterior surface of each tooth strongly concave, so that the three molars are sepa-



FIGURE 1. Photograph of the head of a living *Noctilio leporinus* (courtesy of R. J. Baker).



FIGURE 2. Photograph of a living *Noctilio leporinus*; note the greatly enlarged feet and claws (courtesy of R. J. Baker).

rated by noticeable gaps (unlike condition found in *N. albiventris*). Crown area of third upper molar about half that of second, but also with well-developed cusps, styles, and commissures. Lower molars distinctly sculptured much as the uppers. The dental formula is $i\ 2/1$, $c\ 1/1$, $p\ 1/2$, $m\ 3/3$, total 28. The above description was adapted mostly from Miller (1907).

Geographic variation in size is demonstrable in *N. leporinus* (Davis, 1973); the largest individuals are found in the northern and southern parts of the distribution of the species (subspecies *N. l. mastivus* and *N. l. rufescens*), the smallest in the Amazon Basin (*N. l. leporinus*). Males average larger than females. Average and extreme measurements (mm) for the two sexes in a sample from Chiapas, Mexico (Davis, 1973), are (males followed by females): length of forearm, 85.1 (81.6 to 88.1), 84.5 (81.2 to 87.3); length of third metacarpal, 80.9 (77.5 to 84.6), 79.3 (77.1 to 81.2); condylobasal length, 25.2 (24.7 to 25.9), 24.2 (23.5 to 25.8); zygomatic breadth, 20.0 (19.3 to 20.5), 18.8 (17.8 to 19.6); cranial breadth, 14.7 (14.2 to 15.2), 14.2 (13.7 to 14.7); length of maxillary tooththrow, 10.7 (10.5 to 10.9), 10.3 (10.1 to 10.5); width across M3-M3, 13.7 (13.0 to 13.9), 12.9 (12.5 to 13.2); length of mandible, 19.1 (18.2 to 19.9), 18.3 (17.6 to 18.8); length of mandibular tooththrow (c-m3), 11.6 (10.7 to 11.9), 11.1 (10.8 to 11.5). Traditional external measurements rarely have been given in full in the literature. Ranges (in mm) of those for four females from Dominica, Lesser Antilles, are: total length, 119 to 127; length of tail, 25 to 28; length of hindfoot, 32 to 34; length of ear, 28 to 29.5. Two of these specimens weighed 63.4 and 64.1 g.

As in *Noctilio albiventris*, the pelage is extremely short. Dorsal coloration varies considerably, from pale orange to dark orange, orange brown, brownish, and even grayish brown. A distinct dorsal stripe, whitish to orangish depending on overall dorsal color, extends from between the ears (or farther back in some specimens) to the rump. Variation in color once was thought to represent sexual dichromatism (Allen, 1937) or to be of geographic import, but neither apparently is true (Davis, 1973). Seasonal changes in coloration occur, however, and the paler shades of orange "appear to be the result of wear or bleaching or both" (Davis, 1973:864). Molt has not been studied in adult *N. leporinus*, but is presumably annual as in other bats.

The venter varies in color from whitish to bright orange. The wings and tail membrane are brownish and nearly naked, as are the flanks (reminescent of some mormoopids). The pale brownish ears are furred only at the base.

DISTRIBUTION. This species occurs from western (Sinaloa) and eastern (Veracruz) México, southward to northern Argentina, and is known also from most Caribbean islands. Its distribution is discontinuous in this vast region, restricted mostly to nonarid lowland and coastal areas, and to major river basins such as those of the Amazon and Paraná in South America (Davis, 1973; Figs.



FIGURE 3. Dorsal, ventral, and lateral views of cranium, and lateral view of lower jaw of *Noctilio leporinus* (TTU 31295, ♂) from Montserrat, Lesser Antilles. Greatest length of skull is 27.2 mm.

4 and 5). Baker and Genoways (1978) summarized its distribution in the Antillean region.

FOSSIL RECORD. Fossils of *N. leporinus* are known only from questionably late Pleistocene (probably sub-Recent) cave deposits on Cuba and Puerto Rico (Martin, 1972).

FORM AND FUNCTION. Allen (1889) and Miller (1907) described the postcranial skeleton, especially the bony elements of the wing. Vaughan (1970a, 1970b) and Walton and Walton (1968) discussed functional aspects of the pelvic and pectoral girdles. Smith and Starrett (1979) presented extensive data on wing morphometrics and noted that the wings of *Noctilio albiventris* and *N. leporinus* were essentially identical in shape. In both species, the wing is more than two and a half times the length of the head and body, with nearly 65% of the wingspan composed of the third digit. This attribute, together with a shortened first phalanx in the third and fourth digits, contributes to a relatively high aspect ratio. Although swift flight was associated with high aspect ratios, as described in molossids and emballonurids, Lawlor (1973) and Smith and Starrett (1979) cautioned against such a conclusion regarding *N. leporinus*. Field observation by one of us (JKJ) confirmed that *N. leporinus* has a slow, deliberate wing beat. Strickler (1978) measured shoulder muscle masses and calculated allometric relationships for flight. He concluded that *N. leporinus* was like most other bats in possessing a positive allometric relationship for flight musculature and body mass.

Phillips and Jones (1969) examined 39 specimens for dental abnormalities and found none, but one adult male had lost a right upper incisor in life. Cranial morphology, including cochlear and vomeronasal regions were described by Bhatnagar (1980), Henson (1970), and Pye (1966); these regions are morphologically primitive compared with those found in other microchiropterans, and most closely resemble those found in bats of the family Emballonuridae. Likewise, the hyoid apparatus, including hyoid musculature, is similar to that found in emballonurids (Sprague, 1943).

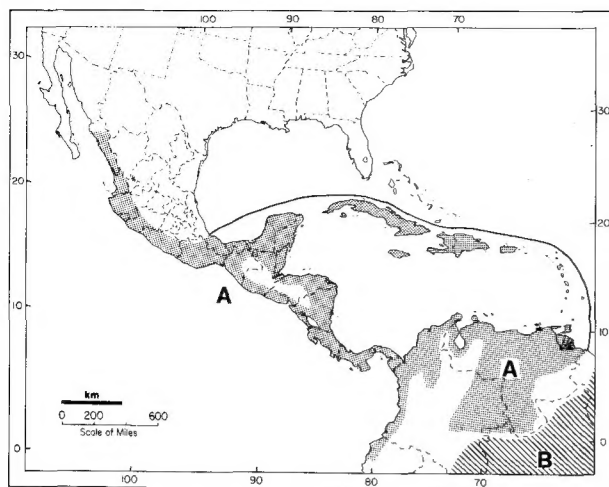


FIGURE 4. Distribution of *Noctilio leporinus* in North America and adjacent regions (principally after Davis, 1973). Subspecies are: A, *N. l. mastivus*; B, *N. l. leporinus*. Bar represents 600 km.

External morphology of the facial region, including the lips, nose pad, and chin, was discussed in comparison with the Mormoopidae and Phyllostomidae by Smith (1972). A detailed illustration of the face can be found in Silva Taboada (1979).

Well-developed cheek pouches are present in both *Noctilio albiventris* and *N. leporinus* (Murray and Strickler, 1975). These are formed by posterolateral expansions of the buccinator muscle and extend caudally to cover a large portion of the masseter. The pouches are used primarily for food storage during foraging; a fish captured by *N. leporinus* is transferred immediately to the mouth where it is partially masticated, then stored in the pouches. This adaptation may allow fishing to continue at a specific locality, thus increasing foraging efficiency. Because *N. albiventris* (primarily insectivorous) also possesses these pouches, Murray and Strickler (1975) suggested that the evolution of piscivory in *N. leporinus* occurred through a hypothetical common ancestor with cheek pouches, but as an adaptation for a diet other than fish.

Morphological and functional adaptations associated with piscivory are found in the digestive tract. Forman (1973) described the morphology and histochemistry of the stomach including a unique modification of the cardiac sphincter that guards the gastroesophageal junction and permits storage of large food items. The musculature of the cardiac sphincter possesses a downward-folding circular layer that, together with an overlying muscularis mucosae forms an anatomically functional valve. Muscle fibers associated with the wall of the sphincter are arranged in complex systems of concentric muscle bundles. Histochemical features of the stomach include an extensive pyloric fundic transition area and a reduction of chief and parietal cells in the fundic caecum. The reduction of chief and parietal cells is a feature observed in many other species of carnivorous bats (*Chrotopterus*, for example). The distribution and structure of lymphatic tissue (Peyer's patches) is similar to that described for other bat species (Forman, 1974a, 1974b).

In comparison with *N. leporinus*, the smaller *N. albiventris* possesses a poorly developed cardiac sphincter consisting of a mere ridge of muscular tissue. Histochemical features of the gastric system in *N. albiventris* are similar to those found in other insectivorous species (Forman, 1972, 1973).

Little information exists concerning general physiology and temperature regulation (McNab, 1969). Basal metabolic rates of *N. leporinus* are typical (adjusting for body weight) compared with those measured in insectivorous microchiropterans, but low compared with other carnivorous bats such as *Chrotopterus*. Silva Taboada (1979) recorded the rectal temperature of bats leaving a daytime roost as averaging 35.9°C for males and 35.4°C for females, and for those returning after foraging as averaging 37.5 and 37.2°C, respectively.

ONTOGENY AND REPRODUCTION. Females of *N. leporinus* are monovular and bear single young each pregnancy. Although detailed reproductive studies have not been undertaken

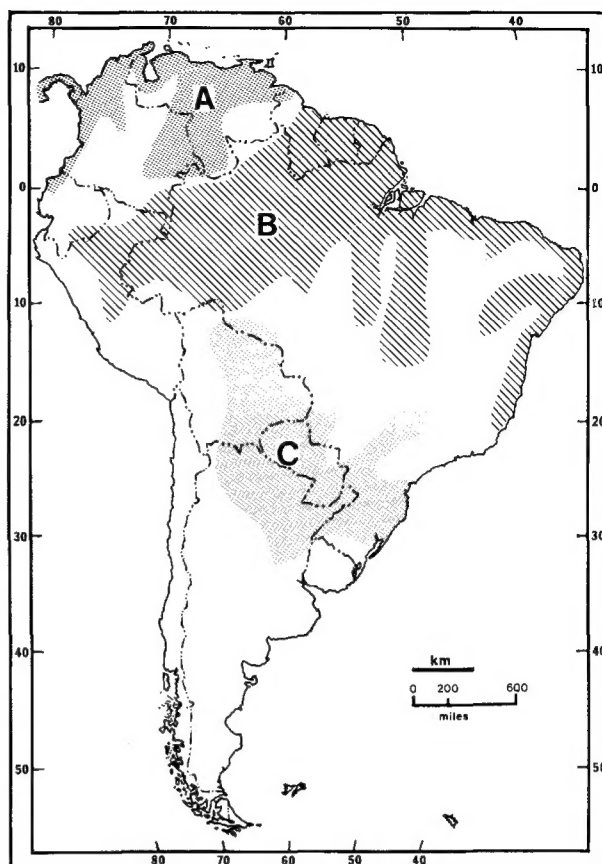


FIGURE 5. Distribution of *Noctilio leporinus* in South America (principally after Davis, 1973). Subspecies are: A, *N. l. mastivus*; B, *N. l. leporinus*; C, *N. l. rufescens*. Bar represents 600 km.

for this species, a large number of reports on field collections document the general seasonal pattern. Few data are available for populations in the Southern Hemisphere, however, and the patterns discussed herein refer to bats occupying Mexico, Central America, and northern South America. Breeding usually begins in November and December with gestation during the winter and early spring, followed by parturition from late April to June. However, a secondary reproductive peak was suggested by some authors on the basis of field data. A postpartum breeding would result in pregnancies during the summer and parturition from October through December (Carter, 1970). Allen (1937) reported 30 gravid females (each with a single large fetus) from a collection of 50 females taken in Panamá in February. Carter et al. (1966) found that each of three females, also collected in Panamá in February, was pregnant. Hooper and Brown (1968) reported three pregnant females (crown-rump length of fetuses 9, 33, 43 mm) from Costa Rica in February. In Nicaragua, Jones et al. (1971) noted pregnancies (crown-rump length 20 and 41 mm) in two of three females taken in March and one lactating female in June.

The pattern of late spring to early summer pregnancy apparently also is typical for populations inhabiting the Greater and Lesser Antilles and Trinidad. Goodwin and Greenhall (1961) reported pregnant females in February, lactating females in late February to March, and nonpregnant females in August on Trinidad. Carter et al. (1981) reported four additional females from that island were not pregnant in July and August. Jones and Baker (1979) collected four females on Montserrat in late July, two of which were lactating. Baker et al. (1978) noted one nonpregnant animal collected on Haiti in January.

Jones et al. (1973) reported on a collection from Campeche, on the Yucatán Peninsula, in which seven females were lactating in July. Additional data for Mexican populations from Jalisco were provided by Watkins et al. (1972), who recorded one pregnant female in April (crown-rump length of fetus 19 mm), one lactating

in January, and three nonpregnant in January and February; J. K. Jones et al. (1972) reported three of seven females lactating in mid-June in Sinaloa. Carter et al. (1966) noted a single pregnant female in February from Guatemala, whereas Dickerman et al. (1981) reported one pregnant female from there in late April and two lactating in September. These latter specimens were cited by Dickerman et al. (1981) as representing the first record of the species breeding in the rainy season (May to September) in Central America. However, these data only document that lactation may continue through early September.

Other authors reported small collections with pregnant individuals in late summer to autumn, suggesting a second reproductive peak in the breeding cycle. Carter et al. (1966) noted three pregnant females from Chiapas taken in October. In addition, Davis et al. (1964) listed two females collected in Veracruz in late December were pregnant with small fetuses. Tuttle (1970) reported two of three females from Perú as pregnant in July (crown-rump length of one fetus 38 mm, another born in captivity).

Despite the possibility of two reproductive peaks for *N. leporinus*, the data must be viewed as largely circumstantial because of limited sample sizes and collection dates. However, a substantial data set was published on *N. leporinus* from Cuba by Silva Taboada (1979), who summarized reproductive information for 264 females collected over several years. Gestation occurred from December to April with large, near-term embryos in April-collected females. Pregnant females were not taken in May or June (samples during these months were small), but a few pregnant animals were captured in July and August; these had extremely small embryos compared with those of females in the April sample. Parturition occurred from late February through October, but most births were observed in late spring and summer. Lactating females were recorded in every month of the year except January; however, most females suckled young during the months of May through September. On the basis of these results, Silva Taboada (1979) concluded that the primary reproductive pattern includes a highly synchronized December breeding with spring and summer births. These data also suggest that a secondary pattern involving a postpartum estrus and autumn winter births is possible.

Reproductive data for male greater bulldog bats generally supports the contention that there is a primary reproductive pattern, with breeding in autumn and winter. Jones et al. (1971) reported four males from Nicaragua with a mean 9.5-mm (range 8 to 10) length of testes in late March and early April. Goodwin and Greenhall (1961) summarized data for males from Trinidad with qualitative descriptions: of two taken in August, one was in breeding and one in nonbreeding condition; in October, 13 of 24 were in breeding condition. Tuttle (1970) collected a male in Perú with 8 by 5 mm testes in July; Jones and Baker (1979) reported two males from Montserrat with testes measuring 6 and 10 mm in July. Birney et al. (1974) noted one young adult (testes 8 mm) from Yucatán in April; J. K. Jones et al. (1972) recorded three males (mid-June) from Sinaloa with testes ranging from 5 to 10 mm in length; Klingener et al. (1978) reported two males with scrotal testes (6 mm) from Haiti in December and January, and one with partially scrotal testes (7 mm) in December.

Silva Taboada (1979) observed a colony in a hollow tree roost for several months following a highly synchronized parturition. Young bats did not leave the roost for their first attempts at sustained flight until they had reached nearly full adult size at slightly less than 1 month of age. Adult males and females remained at the roost throughout this time, suggesting that a high degree of parental care may be characteristic of this species.

Elaborate breeding behavior is not known in *N. leporinus*. An unusual pocket-like fold of skin is associated with the scrotum in males (Dunn, 1934; Goodwin and Greenhall, 1961). Glands associated with the pocket apparently are responsible for the musky odor noticeable in males.

ECOLOGY AND BEHAVIOR. The species found most commonly in tropical lowland habitats (Bloedel, 1955; Carter et al., 1966; Davis et al., 1964; Goodwin, 1946; J. K. Jones et al., 1971, 1972; Watkins et al., 1972). These bats were observed and captured most frequently over ponds and quiet streams, but also were found associated with estuaries of major rivers and in bays and lagoons along coastlines (Baker et al., 1978; Benedict, 1926; Goodwin, 1928; Goodwin and Greenhall, 1961; Gudger, 1945; Jones and Baker, 1979; Klingener et al., 1978; Smith and Genoways,

1974). Koopman (1968) noted that although collections of bats from the Lesser Antilles contained relatively few specimens of *N. leporinus*, the species likely was to be found anywhere throughout the region where fresh or salt water was calm enough to allow it to fish (Baker and Genoways, 1978).

Greater bulldog bats roost in colonies that may number up to several hundred individuals. Goodwin and Greenhall (1961) reported that colonies were found most frequently on Trinidad in hollow trees, including silk-cotton (*Ceiba pentandra*), red mangrove (*Rhizophora mangle*), and balata (*Manilkara bidentata*). *Desmodus rotundus* was the only bat reported to co-occupy such roosts. The hollow tree roosts of one colony of 75 individuals on Trinidad, contained within the trunk of a *Ceiba pentandra*, was examined in detail by Goodwin and Greenhall (1961). The roost extended upward about 10 m; the bats occupied the uppermost 5 m of the hollow. The interior was dark, humid, and permeated with a strong odor of fish.

Males and females, as well as juveniles and adults, were found together in hollow tree roosts in México (Jones et al., 1973), on Hispanola (Armstrong and Johnson, 1969), and on Cuba (Silva Taboada, 1979). However, Carter et al. (1966) reported that 16 individuals (all males) were found in a large hollow tree in Honduras; these were spaced a minimum distance of 20 cm apart (mean was 30 cm). In addition, Dickerman et al. (1981) monitored two hollow tree roosts in Guatemala that were used predominantly by immature individuals. On Trinidad, Goodwin and Greenhall (1961) found the sexes were segregated at the time of parturition, but roosted together throughout the remainder of the year.

Greater bulldog bats also utilize dark sea caves as roosts (Goodwin, 1946; Goodwin and Greenhall, 1961; Silva Taboada, 1979). On Trinidad, *N. leporinus* was found in sea caves in association with *Mormoops megalophylla*, *Glossophaga soricina*, *Carollia perspicillata*, and *Desmodus rotundus*. Silva Taboada (1979) noted that *Pteronotus*, *Mormoops*, *Brachyphylla*, and *Monophyllus* shared sea cave roosts with *N. leporinus* on Cuba.

Noctilio leporinus is one of a few bats to have evolved a fish-eating habit. This feeding strategy was investigated by numerous workers and generated considerable debate regarding whether or not these bats were capable of catching fish (Bloedel, 1955; Goodwin, 1928; Gudger, 1945). Modifications in functional morphology found in *N. leporinus* strongly suggest a fishing habit. These include greatly elongated feet, claws, and calcar (Fig. 2), a formidable dental arcade, cheek pouches, and specializations in gastric morphology and histochemistry. However, analyses of stomach contents provided evidence that fish are not taken exclusively. Although remains of fish were found in the stomachs of most bats examined, large amounts of insect material also were reported (Goodwin, 1928; Gudger, 1945). Insect prey include winged ants (*Solenopsis* sp.), molecrickets (*Gryllotalpa* sp.), beetles (Scarabaeidae), cerambycids (*Lagochirus araneiformis*), elaterids (*Pyrophorus* sp.), cockroaches (Blattidae), and stink bugs (*Thyanta* sp.) (Fleming et al., 1972; Goodwin, 1928, 1946; Goodwin and Greenhall, 1961; Hooper and Brown, 1968). Silva Taboada (1979) reported a diversity of beetles (Carabidae, *Clivina* sp.; Dytiscidae, *Thermonetus circumscripta*; Hydrophilidae, *Hydrophilus intermedius*), and Orthoptera (Gryllidae) from stomach contents of these bats from Cuba.

Observations on hunting behavior document that greater bulldog bats skim the surface of ponds and quiet streams (Bloedel, 1955; Goodwin and Greenhall, 1961), and waters of protected estuarine areas and salt-water bays. Bloedel (1955) provided compelling photographic evidence that the species indeed catches fish by gaffing them with the massive claws. A number of investigators have studied how *N. leporinus* detects fish to initiate the hunting behavior. Bloedel (1955) proposed that bats randomly "drag" over ponds with high prey density, whereas Griffin and Novick (1955) thought they located prey species beneath the surface by echolocation. Suthers (1965) found that *N. leporinus* actively searched for fish and detected them at the surface. Bats were unable to detect completely submerged prey, but could register on extremely minute disturbances on the surface. Vision and olfaction are not necessary to locate prey; echolocation serves as the primary means of doing so. Detection and capture of prey (including insects) from water surfaces also were observed in other bat species suspected of catching fish, such as *Pizonyx vivax* and *Noctilio albiventris* (Novick and Dale, 1971; Suthers, 1967; Suthers and Fattu, 1973).

Two distinct echolocation sounds are emitted during flight (Suthers, 1965). In one, constant frequency (CF) pulses begin at 60 kHz, but may have a terminal downward sweep in frequency

that does not drop below 50 kHz. A second pulse type involves a CF beginning at about 60 kHz that is modulated downward in frequency more than one octave. Both of these echolocatory pulses have a duration of about 8 ms for captive bats (bats monitored in the wild had 14 ms pulses according to Suthers, 1965). In pursuing prey, repetition rates increase from 16 to 200/s and the constant frequency portions all are frequency modulated. Pulse durations decreased further to about 1 ms in the final approach and capture phases. Griffin and Novick (1955) noted that ultrasonic cries of *N. leporinus* generally were like those produced by other microchiropterans. However, the CF and FM patterns of *N. leporinus* are adapted to long range sonar, features that may optimize their fish-catching abilities (Novick, 1977).

Activity patterns of *Noctilio leporinus* differ significantly from those of its congener, *N. albiventris* (Brown, 1968; Hooper and Brown, 1968). Whereas *N. albiventris* has well-defined early and late activity peaks, the greater bulldog bat apparently is active throughout the night (Silva Taboada, 1979). Hooper and Brown (1968) suggested that differences in nocturnal activity contributed to differences in diet and reproduction that allowed coexistence of the two species. Silva Taboada (1979) monitored the activity patterns of a large colony in Cuba for a year. Although he noted that *N. leporinus* was active throughout the night, it varied seasonally in the time of emergence from the roost. When ambient temperatures dropped in October, November, and December, the bats became active at least 2 h earlier than in warmer months.

Noctilio leporinus was captured (by mist net) in association with *Rhynchonycteris naso*, *Saccopteryx bilineata*, *Balantiopteryx plicata*, *Pteronotus personatus*, *Glossophaga soricina*, *Sturmira lilium*, *Chiroderma improvisum*, *Artibeus jamaicensis*, *A. toltecus*, *Ardops nichollsi*, *Phyllops haitensis*, *Centurio senex*, *Brachyphyllum cavernarum*, *Rhogeessa parvula*, *Molossus ater*, and *M. molossus* (Armstrong and Johnson, 1969; Birney et al., 1974; Jones and Baker, 1979; Starrett and Casebeer, 1968; Watkins et al., 1972).

Ectoparasites and endoparasites of *N. leporinus* include ticks, mites, batflies, nematodes, and trematodes. A spinturnicid mite, *Periglischrus aitheni*, was found on a specimen from Panamá (Furman, 1966), and Herrin and Tipton (1975) reported *P. oajasti* from specimens taken in Venezuela. McDaniel (1972) recorded two species of labidocarpid mites, *Parakosa maxima* and *P. tadarida*, from bulldog bats in Venezuela. *Chiroptonyssus venezolanus* (Macronyssidae) was collected from *N. leporinus* on Cuba, but this mite occurs primarily on molossids (Dusbabek, 1969). Other acarines recorded from bulldog bats from Cuba (Silva Taboada, 1979) include *Ornithodoros dusbabeki* (Argasidae), and *Notoedres noctilionis* (Labidocarpidae). Goodwin and Greenhall (1961) reported mites (*Teinocopterus* sp., Sarcoptidae), batbugs (*Latrocimex* sp., Cimicidae), and unidentified trematodes for bats from Trinidad. Silva Taboada (1979) noted a trematode, *Pygidiopsis macrostomum*, and nematodes, *Contracaecum* sp., *Tricholeiperia proencai*, *Spirocerca lupi*, and *Capillaria viguerasi*, from Cuban specimens.

Batflies (Streblidae) that regularly parasitize *N. leporinus* include *Noctiliostrebla aitheni*, *N. dubia*, *N. megastimata*, *N. traubi*, *Paradyschiria fusca*, *P. lineata*, and *Xenotrichobius noctilionis* (Wenzel, 1976; Wenzel et al., 1966); flies of several other genera were reported but listed as not normally parasitizing the greater bulldog bat. The three streblid genera listed are characteristic of, if not restricted to, *Noctilio*. In addition, Fairchild et al. (1966) reported a tick, *Ornithodoros hasei* (Argasidae) on *N. leporinus* from Panamá, and E. K. Jones et al. (1972) recorded that species, *O. boliviensis*, and *O. tiptoni* from Venezuelan specimens. Ueshima (1972) reported a specimen of *Hesperoctenes fumarius* (Hemiptera, Polycetidae) from a *N. leporinus* from Venezuela but opined that the association probably was accidental.

Fischthal and Martin (1978) described a new species of digenetic trematode, *Postorchigenes paraguayensis*, from the small intestine of one of 23 *N. leporinus* examined from Paraguay.

Rabies has not been found in wild populations of this fishing bat. However, *Histoplasma capsulatum*, the infective agent for histoplasmosis, was isolated from the hollow tree roosts of *N. leporinus* on Trinidad (Goodwin and Greenhall, 1961).

GENETICS. The standard karyotype (Fig. 6) of *Noctilio leporinus* ($2n = 34$, $FN = 58$) contains a graded series of 13 pairs of submetacentric and three pairs of acrocentric autosomes, with a medium-sized metacentric X and a small acrocentric Y chromosome

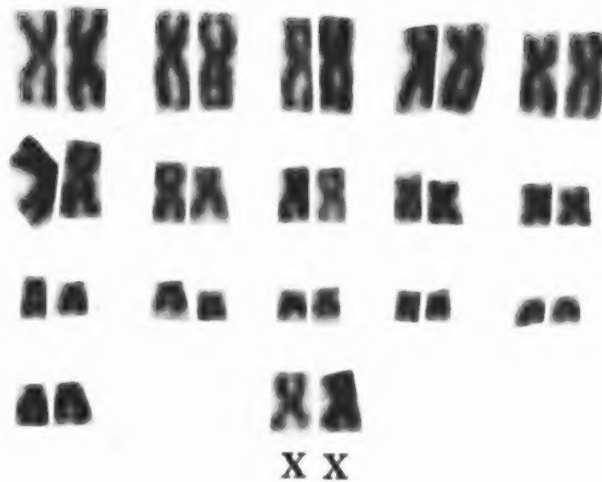


FIGURE 6. Karyotype of a female *Noctilio leporinus* (TTU 17921) from Oelemarie, Marowijne, Suriname.

(Baker, 1970; Yonenaga et al., 1969). Subsequent G- and C-banding studies led to a revision of the fundamental number to 62 (Baker and Bickham, 1980; Baker et al., 1982; Patton and Baker, 1978). C-band analysis shows that heterochromatin is restricted to the centromere in all elements except chromosome 29 (Baker et al., 1982; Patton and Baker, 1978). The chromosomal complement of *N. leporinus* is identical with that found in *N. albiventris*.

Comparisons of the karyotypes of *N. leporinus* and *N. albiventris* with those of bats of the family Mormoopidae illustrate extensive chromosomal homology among members of these two families. Noctilionids and mormoopids illustrate the least amount of chromosomal differentiation thus far documented between two families of bats (Baker and Bickham, 1980; Sites et al., 1981).

Genic relationships of *Noctilio leporinus* to *N. albiventris*, mormoopids and phyllostomids were assessed by use of protein electrophoretic and albumin immunological data (Arnold et al., 1982). No allozymic or immunological differences were detected between the two species of *Noctilio*, yet relationships to mormoopids and phyllostomids were less well resolved.

REMARKS. Phylogenetic relationships of noctilionids have been debated for many years. Most early classifications placed them in association with emballonurids; this resulted in the family being assigned to the superfamily Emballonuroidea (Dobson, 1875; Miller, 1907; Simpson, 1945; Trouessart, 1897). However, this arrangement apparently was based mostly on shared primitive features. Other workers proposed a close relationship of noctilionids with mormoopids and phyllostomids and placed these three families in a monophyletic superfamily Phyllostomoidea on the basis of shared derived features (Arnold et al., 1982; Hood and Smith, 1982; Patton and Baker, 1978; Smith, 1972; Walton and Walton, 1968; Winge, 1892).

Noctilio leporinus also is known in the vernacular as the fishing bat.

LITERATURE CITED

- Allen, G. M. 1937. Sex dichromatism in *Noctilio*. J. Mamm., 18: 514.
- Allen, H. 1889. On the taxonomic value of the wing-membranes and of the terminal phalanges of the digits of the Cheiroptera. Proc. Acad. Nat. Sci. Philadelphia, 41:313-340.
- Armstrong, F. H., and M. L. Johnson. 1969. *Noctilio leporinus* in Hispanola. J. Mamm., 50:133.
- Arnold, M. L., et al. 1982. Resolving a phylogeny with multiple data sets: a systematic study of phyllostomid bats. Occas. Papers Mus., Texas Tech Univ., 77:1-15.
- Baker, R. J. 1970. Karyotypic trends in bats. Pp. 65-96, in Biology of bats (W. A. Wimsatt, ed.). Academic Press, New York, 1:xii + 1-406.
- Baker, R. J., and J. W. Bickham. 1980. Karyotypic evolution in bats: evidence of extensive and conservative chromosomal evolution in closely related taxa. Syst. Zool., 29:239-253.

- Baker, R. J., and H. H. Genoways. 1978. Zoogeography of Antillean bats. Pp. 53-97, in *Zoogeography in the Caribbean* (F. B. Gill, ed.). Spec. Publ. Acad. Nat. Sci. Philadelphia, 13: 1-128.
- Baker, R. J., H. H. Genoways, and J. C. Patton. 1978. Bats of Guadeloupe. *Occas. Papers Mus., Texas Tech Univ.*, 50:1-16.
- Baker, R. J., et al. 1982. Chromosomal studies of South American bats and their systematic implications. Pp. 303-327, in *Mammalian biology in South America* (M. A. Mares and H. H. Genoways, eds.). Spec. Publ. Ser., Pymatuning Ecol. Lab., 6:xii + 1-539.
- Benedict, J. E. 1926. Notes on the feeding habits of *Noctilio*. *J. Mamm.*, 7:58-59.
- Bhatnagar, K. P. 1980. The chiropteran vomeronasal organ: its relevance to the phylogeny of bats. Pp. 289-315, in *Proc. Fifth Internatl. Bat Res. Conf.* (D. E. Wilson and A. L. Gardner, Eds.). Texas Tech Press, Lubbock, 434 pp.
- Birney, E. C., J. B. Bowles, R. M. Timm, and S. L. Williams. 1974. Mammalian distributional records in Yucatan and Quintana Roo, with comments on reproduction, structure, and status of peninsular populations. *Occas. Papers Bell Mus. Nat. Hist., Univ. Minnesota*, 13:1-25.
- Bloedel, P. 1955. Hunting methods of fish-eating bats, particularly *Noctilio leporinus*. *J. Mamm.*, 36:390-399.
- Brown, J. H. 1968. Activity patterns of some neotropical bats. *J. Mamm.*, 49:754-757.
- Carter, C. H., H. H. Genoways, R. S. Loregnard, and R. J. Baker. 1981. Observations on bats from Trinidad, with a checklist of species occurring on the island. *Occas. Papers Mus., Texas Tech Univ.*, 72:1-27.
- Carter, D. C. 1970. Chiropteran reproduction. Pp. 233-246, in *About bats* (B. H. Slaughter and D. W. Walton, eds.). Southern Methodist Univ. Press, Dallas, vii + 339 pp.
- Carter, D. C., R. H. Pine, and W. B. Davis. 1966. Notes on Middle American bats. *Southwestern Nat.*, 11:488-499.
- Davis, W. B. 1973. Geographic variation in the fishing bat, *Noctilio leporinus*. *J. Mamm.*, 54:862-874.
- 1976. Geographic variation in the lesser noctilio, *Noctilio albiventris* (Chiroptera). *J. Mamm.*, 57:687-707.
- Davis, W. B., D. C. Carter, and R. H. Pine. 1964. Noteworthy records of Mexican and Central American bats. *J. Mamm.*, 45:375-387.
- Desmarest, A. G. 1818. Article ["Noctilion ou bec de lievre"]. *Nouv. Dict. d'Hist. Nat.*, 23:14-16.
- Dickerman, R. W., K. F. Koopman, and C. Seymour. 1981. Notes on bats from the Pacific lowlands of Guatemala. *J. Mamm.*, 62:406-411.
- Dobson, G. E. 1875. Conspectus of the suborders, families, and genera of Chiroptera arranged according to their natural affinities. *Ann. Mag. Nat. Hist., ser. 4*, 16:345-357.
- D'Orbigny, A. 1835. Voyage dans l'Amerique Meridionale. . . Atlas Zool., Mammiferas, pl. 9, figs. 1-4.
- Dunn, L. H. 1934. Notes on the little bulldog bat, *Dirias albiventer minor* (Osgood), in Panama. *J. Mamm.*, 15:89-99.
- Dusabek, F. 1969. Macronyssidae (Acarina: Mesostigmata) of Cuban bats. *Folia Parasitol.*, 16:321-328.
- Fairchild, G. B., G. M. Kohls, and V. J. Tipton. 1966. The ticks of Panama. Pp. 167-219, in *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, xii + 861 pp.
- Fermin, P. 1765. *Historie naturelle de la Hollande équinoxiale*. . . Amsterdam, xii + 240 pp.
- Fischthal, J. H., and R. L. Martin. 1978. *Postorchigenes paraguayensis* sp. n. (Trematoda, Pleurogenidae), a digenetic trematode from a large fishing bat, *Noctilio leporinus rufescens* Olfers, from Paraguay. *Acta Parasitol. Polonica*, 25: 217-221.
- Fleming, T. H., E. T. Hooper, and D. C. Wilson. 1972. Three Central American bat communities: structure, reproductive cycles, and movement patterns. *Ecology*, 53:555-569.
- Forman, G. L. 1972. Comparative morphological and histochemical studies of stomachs of selected American bats. *Univ. Kansas Sci. Bull.*, 49:591-729.
- 1973. Studies of gastric morphology in North American Chiroptera (Emballonuridae, Noctilionidae, Phyllostomatidae). *J. Mamm.*, 54:909-923.
- 1974a. Comparative studies of organized gut-associated lymphoid tissue in mammals with diverse food habits; distribution, size, and organization of Peyer's patches in New World bats. *Trans. Illinois State Acad. Sci.*, 67:152-162.
- 1974b. Structure of Peyer's patches and their associated nodules in relation to food habits of New World bats. *J. Mamm.*, 55:738-746.
- Furman, D. P. 1966. The spinturnicid mites of Panama. Pp. 125-166, in *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, xii + 861 pp.
- Goodwin, G. G. 1928. Observations on *Noctilio*. *J. Mamm.*, 9: 93-113.
- 1946. Mammals of Costa Rica. *Bull. Amer. Mus. Nat. Hist.*, 87:275-474.
- Goodwin, G. G., and A. M. Greenhall. 1961. A review of the bats of Trinidad and Tobago. *Bull. Amer. Mus. Nat. Hist.*, 122:187-301.
- Griffin, D. R., and A. Novick. 1955. Acoustic orientation of neotropical bats. *J. Exp. Zool.*, 130:251-300.
- Griffith, E., et al. 1827. The animal kingdom, arranged in conformity with its organization. . . G. B. Whittaker, London, 5 vols. (J. E. Gray's listing of *Noctilio* in vol. 5, p. 67).
- Gudger, E. W. 1945. Fisherman bats of the Caribbean region. *J. Mamm.*, 26:1-15.
- Henson, O. W. 1970. The ear and audition. Pp. 181-263, in *Biology of bats* (W. A. Wimsatt, ed.). Academic Press, New York, 2:xv + 1-477.
- Herrin, C. S., and V. J. Tipton. 1975. Spinturnicid mites of Venezuela (Acarina: Spinturnicidae). *Brigham Young Univ. Sci. Bull.*, 20(2):1-72.
- Hershkovitz, P. 1949. Mammals of northern Colombia. Preliminary report no. 5: bats (Chiroptera). *Proc. U.S. Natl. Mus.*, 99:429-454.
- 1975. The scientific name of the lesser *Noctilio* (Chiroptera), with notes on the chauve-souris de la Vallée d'Ylo (Peru). *J. Mamm.*, 56:242-247.
- Hood, C. S., and J. Pitocchelli. 1983. *Noctilio albiventris*. *Mamm. Species*, 197:1-5.
- Hood, C. S., and J. D. Smith. 1982. Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. *Syst. Zool.*, 31:241-251.
- Hooper, E. T., and J. H. Brown. 1968. Foraging and breeding in two sympatric species of neotropical bats, genus *Noctilio*. *J. Mamm.*, 49:310-312.
- Jones, E. K., C. M. Clifford, J. E. Keirans, and G. M. Kohls. 1972. The ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of *Amblyomma* in the Western Hemisphere. *Brigham Young Univ. Sci. Bull.*, 17(4):1-40.
- Jones, J. K., Jr., and R. J. Baker. 1979. Notes on a collection of bats from Montserrat, Lesser Antilles. *Occas. Papers Mus., Texas Tech Univ.*, 60:1-6.
- Jones, J. K., Jr., J. R. Choate, and A. Cadena. 1972. Mammals from the Mexican State of Sinaloa. II. Chiroptera. *Occas. Papers Mus. Nat. Hist., Univ. Kansas*, 6:1-29.
- Jones, J. K., Jr., J. D. Smith, and H. H. Genoways. 1973. Annotated checklist of mammals of the Yucatan Peninsula, Mexico. I. Chiroptera. *Occas. Papers Mus., Texas Tech Univ.*, 13:1-31.
- Jones, J. K., Jr., J. D. Smith, and R. W. Turner. 1971. Noteworthy records of bats from Nicaragua, with a checklist of the chiropteran fauna of the country. *Occas. Papers Mus. Nat. Hist., Univ. Kansas*, 2:1-35.
- Kerr, R. 1792. The animal kingdom. . . London, xii + (14) + 400 pp.
- Klingener, D., H. H. Genoways, and R. J. Baker. 1978. Bats from southern Haiti. *Ann. Carnegie Mus. Nat. Hist.*, 47:81-99.
- Koopman, K. F. 1968. Taxonomic and distributional notes on Lesser Antillean bats. *Amer. Mus. Novitates*, 2333:1-13.
- Lawlor, T. E. 1973. Aerodynamic characteristics of some neotropical bats. *J. Mamm.*, 54:71-78.
- Leach, W. E. 1821. The characters of three new genera of bats without foliaceous appendages to the nose. *Trans. Linnaean Soc. London*, 13:69-72.
- Linnaeus, C. 1758. *Systema naturae*. . . Holmiae, ed. 10, 1:1-824.
- 1766. *Systema naturae*. . . Holmiae, ed. 12, 1(1):1-532.

- Martin, R. A. 1972. Synopsis of late Pliocene and Pleistocene bats of North America and the Antilles. *Amer. Midland Nat.*, 87:326-335.
- McDaniel, B. 1972. Labidocarpid bat-mites of Venezuela (Lisrophoroidea: Labidocarpidae). *Brigham Young Univ. Sci. Bull.*, 17(2):15-32.
- McNab, B. K. 1969. The economics of temperature regulation in neotropical bats. *Comp. Biochem. Physiol.*, 31:227-268.
- Miller, G. S., Jr. 1906. Twelve new genera of bats. *Proc. Biol. Soc. Washington*, 19:83-86.
- 1907. The families and genera of bats. *Bull. U.S. Natl. Mus.*, 57:1-282.
- Murray, P. F., and T. Strickler. 1975. Notes on the structure and function of cheek pouches within the Chiroptera. *J. Mamm.*, 56:673-676.
- Novick, A. 1977. Acoustic orientation. Pp. 73-287, in *Biology of bats* (W. A. Wimsatt, ed.). Academic Press, New York, 3: xvi + 1-651.
- Novick, A., and B. A. Dale. 1971. Foraging behavior in fishing bats and their insectivorous relatives. *J. Mamm.*, 52:817-818.
- Olfers, I. von. 1818. Bemerkungen zu Illiger's Ueberblick der Säugthiere nach ihrer Vertheilung über die Welttheile, rück-sichtlich Südamerikanischen Arten (chapter 10 in W. L. Eschwege's *Journal von Brasilien*). *Neue Bibliothek. . .*, 15(2): 192-237.
- Patton, J. C., and R. J. Baker. 1978. Chromosomal homology and evolution of phyllostomatoid bats. *Syst. Zool.*, 27:449-462.
- Phillips, C. J., and J. K. Jones, Jr. 1969. Dental abnormalities in North American bats. I. Emballonuridae, Noctilionidae, and Chilonycteridae. *Trans. Kansas Acad. Sci.*, 71:509-520.
- Pye, A. 1966. The structure of the cochlea in Chiroptera. I. Microchiroptera: Emballonuroidea and Rhinolophoidea. *J. Morph.*, 118:495-510.
- Schinz, H. R. 1821. *Das Thierreich. . .* Stuttgart and Tübingen, 1:xxxviii + 1-894.
- Silva Taboada, G. 1979. Los murciélagos de Cuba. *Acad. Cien. Cuba, Havana*, xiii + 423 pp.
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 85:xvi + 1-350.
- Sites, J. W., J. W. Bickham, and M. W. Haiduk. 1981. Conservative chromosomal change in the bat family Mormoopidae. *Canadian J. Genet. Cytol.*, 23:459-467.
- Smith, J. D. 1972. Systematics of the chiropteran family Mormoopidae. *Misc. Publ. Mus. Nat. Hist., Univ. Kansas*, 56:1-132.
- Smith, J. D., and H. H. Genoways. 1974. Bats of Margarita Island, Venezuela, with zoogeographic comments. *Bull. S. California Acad. Sci.*, 73:64-79.
- Smith, J. D., and A. Starrett. 1979. Morphometric analysis of chiropteran wings. Pp. 229-316, in *Biology of bats of the New World family Phyllostomatidae*, Part 3 (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). *Spec. Publ. Mus., Texas Tech Univ.*, 16:1-441.
- Spix, J. 1823. *Simiarum et vespertilionum brasiliensium species novae. . .* Munich, (8) + viii + 72 pp.
- Sprague, J. M. 1943. The hyoid region of placental mammals with especial reference to the bats. *Amer. J. Anat.*, 72:385-472.
- Starrett, A., and R. S. Casebeer. 1968. Records of bats from Costa Rica. *Contrib. Sci., Los Angeles Co. Mus.*, 148:1-21.
- Strickler, T. L. 1978. Allometric relationships among the shoulder muscles in the Chiroptera. *J. Mamm.*, 59:36-44.
- Suthers, R. A. 1965. Acoustic orientation by fish-catching bats. *J. Exp. Zool.*, 158:319-348.
- 1967. Comparative echolocation by fishing bats. *J. Mamm.*, 48:79-87.
- Suthers, R. A., and A. Fattu. 1973. Fishing behavior and acoustic orientation by the bat (*Noctilio labialis*). *Anim. Behav.*, 21: 61-66.
- Thomas, O. 1911. The mammals of the tenth edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. *Proc. Zool. Soc. London*, pp. 120-158.
- Trouessart, E. L. 1897. *Catalogue mammalium tam viventium quam fossilium. Nova editio (prima completa)*. R. Friedlander and Sohn, Berlin, 1:1-218.
- Tuttle, M. D. 1970. Distribution and zoogeography of Peruvian bats, with comments on natural history. *Univ. Kansas Sci. Bull.*, 49:45-86.
- Ueshima, N. 1972. New World Polyctenidae (Hemiptera), with special reference to Venezuelan species. *Brigham Young Univ. Sci. Bull.*, 17(1):13-21.
- Vahl, M. 1797. *Beskrivelse paa tre nye Arter Flagermuse*. *Skriv. Naturhist.-Selskabet Kjobenhavn*, 4:121-138.
- Vaughan, T. A. 1970a. The skeletal system. Pp. 97-138, in *Biology of bats* (W. A. Wimsatt, ed.). Academic Press, New York, 1:xii + 1-406.
- 1970b. Flight patterns and aerodynamics. Pp. 195-216, in *Biology of bats* (W. A. Wimsatt, ed.). Academic Press, New York, 1:xii + 1-406.
- Walton, D. W., and G. W. Walton. 1968. Comparative osteology of the pelvic and pectoral girdles of the Phyllostomatidae (Chiroptera: Mammalia). *J. Grad. Res. Center, Southern Methodist Univ.*, 37:1-35.
- Watkins, L. C., J. K. Jones, Jr., and H. H. Genoways. 1972. Bats of Jalisco, México. *Spec. Publ. Mus., Texas Tech Univ.*, 1:1-44.
- Wenzel, R. L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). *Brigham Young Univ. Sci. Bull.*, 20(4):1-177.
- Wenzel, R. L., V. J. Tipton, and A. Kiewlicz. 1966. The streblid batflies of Panama (Diptera Calyptræ: Streblidae). Pp. 405-675, in *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton, eds.). *Field Mus. Nat. Hist., Chicago*, xii + 861 pp.
- Winge, H. 1892. *Jordfundne og nulevende Flagermus (Chiroptera) fra Lagon Santa, Minas Geras, Brasilien*. *Mus. Lundii, Kjobenhavn*, 2:1-65.
- Yonenaga, Y., O. Frota-Pessoa, and K. R. Lewis. 1969. Karyotypes of seven species of Brazilian bats. *Caryologia*, 22:63-79.

Editors of this account were SYDNEY ANDERSON and B. J. VERTS. Managing editor was TIMOTHY E. LAWLOR.

C. S. HOOD AND J. K. JONES, JR., THE MUSEUM AND DEPARTMENT OF BIOLOGICAL SCIENCES, TEXAS TECH UNIVERSITY, LUBBOCK 79409.